Minimizing inbreeding by managing genetic contributions across generations

Minimizing Inbreeding by Managing Genetic Contributions Across Generations

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ABSTRACT

Here we present the strategy that achieves the lowest possible rate of inbreeding (ΔF) for a population with unequal numbers of sires and dams with random mating. This new strategy results in a ΔF as much as 10% lower than previously achieved. A simple and efficient approach to reducing inbreeding in small populations with sexes of unequal census number is to impose a breeding structure where parental success is controlled in each generation. This approach led to the development of strategies for selecting replacements each generation that were based upon parentage, *e.g.*, a son replacing its sire. This study extends these strategies to a multigeneration *round robin* scheme where genetic contributions of ancestors to descendants are managed to remove all uncertainties about breeding roles over generations; *i.e.*, male descendants are distributed as equally as possible among dams. In doing so, the sampling variance of genetic contributions within each breeding category is eliminated and consequently ΔF is minimized. Using the concept of long-term genetic contributions, the asymptotic ΔF of the new strategy for random mating, M sires and d dams per sire, is $\phi/(12M)$, where $\phi = [1 + 2(1/4)^d]$. Predictions were validated using Monte Carlo simulations. The scheme was shown to achieve the lowest possible ΔF using pedigree alone and showed that further reductions in ΔF below that obtained from random mating arise from preferential mating of relatives and not from their avoidance.

DIVERSITY within a population is an essential part of global biodiversity in wildlife (Saccheri *et al.* 1998; Frankham *et al.* 2002) and in domestic species (FAO 1998; Weiner *et al.* 1992). The critical measure of the rate of loss of genetic diversity within a population is the rate of inbreeding (ΔF; Hartl and Clark 1989). To maintain genetic diversity and avoid extinction, it is essential to minimize ΔF in small populations, such as zoo populations or rare domestic breeds (Grundy *et al.* 1998a; Frankham 1999). The classical solution to this problem requires equal numbers of breeding males and females (Wright 1938). Many populations, however, show harem structures with highly skewed mating ratios, and often there are difficulties in managing large numbers of mature breeding males.

It was long believed that the lowest ΔF in populations with unequal numbers of breeding males and females was achieved by a breeding system in which a son replaced its sire and a daughter replaced her dam (Gowe *et al.* 1959). Thus every dam has one breeding daughter, and as many dams as sires have also one breeding son (such dams are termed dams of sires hereafter). This breeding system has the effect of reducing the variance of family size, and it is an extension of the classical solution for equal numbers of breeding males and females (Wright 1938). Wang (1997) showed that the strategy of Gowe *et al.* (1959) could be significantly improved upon, by not allowing the dam of sire to also have a breeding daughter, but instead allowing another dam to have an extra breeding daughter. Such strategies are effective and have provided the basic framework for successfully managing populations. Yet they consider only one generation at the time of selection and mating.

Here we derive the minimum possible ΔF for populations with unequal numbers of breeding males and females, by optimizing selection decisions considering multiple generations. The development of pedigrees over multiple generations can be modeled by using the concept of long-term genetic contributions (Wray and Thompson 1990; Woolliams *et al.* 1999; Woolliams and Bijma 2000). In this study we show that management of long-term genetic contributions of breeding individuals across generations is the key to minimizing ΔF. We establish a lower bound for ΔF and present a simple solution that achieves this bound. We derive the expression for the asymptotic ΔF of the new scheme. Results are compared with those of Gowe *et al.* (1959) and Wang (1997), and the theory was validated using Monte Carlo simulation.

MATERIALS AND METHODS

Notation: See Table 1 for a description of the main notational conventions.

Minimizing rates of inbreeding: With random mating, the rate of inbreeding is

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TABLE 1

Notation used for derivation of expressions

c_i	Observed contribution to next generation of individual i
r_i	Observed long-term contribution of individual i
Category j	Breeding group of same sex with same c or r
μ_j, σ_j^2	Expectation and variance of r_i for parent in category j
μ_F, σ_F^2	Expectation and variance of r_i for a female parent
μ_M, σ_M^2	Expectation and variance of r_i for a male parent
X_j	Number of parents in category j
M, F	Total number of male and female parents per generation ($F \geq M$)
d	$d = F/M$, number of females mated to a single male
$E[Z]$, $V[Z]$	Denotes expectation and variance of a random variable Z
$E[Z\|Y]$, $V[Z\|Y]$	Denotes conditional expectation and variance of Z given Y

$$\Delta F = \frac{1}{4}\sum_{i=1}^{N} r_i^2, \tag{1}$$

where r_i is the long-term genetic contribution of breeding individual i and the sum is taken over all N breeding individuals in a generation (Wray and Thompson 1990; Woolliams and Bijma 2000). The long-term contribution measures the ultimate contribution of a breeding individual to the gene pool, expressed as a proportion $r_i \in [0 \ldots 1]$. Per generation, long-term contributions sum to a value of 1, $\Sigma_{i=1}^{N} r_i = 1$ (Woolliams *et al.* 1999). Therefore, to minimize inbreeding on a per generation basis, the problem is to minimize $\Sigma_{i=1}^{N} r_i^2$, given that $\Sigma_{i=1}^{N} r_i = 1$. Since $E(r^2) = E(r)^2 + \sigma_r^2$ and $E(r) = 1/N$, this problem is equivalent to minimizing σ_r^2. In the following we derive σ_r^2 for two existing breeding schemes and derive the breeding scheme that minimizes σ_r^2, which is the scheme with the lowest possible ΔF.

Breeding systems and their ΔF: The classical solution to minimize ΔF has equal numbers of breeding males (M) and females (F) per generation, $M = F = \frac{1}{2}N$, and each breeding pair contributes exactly two offspring to the next generation. In this scheme, the long-term contribution of each breeding individual is $1/N$, the variance of long-term contributions is zero, and ΔF is $1/(4N)$ (Wright 1938).

A rate of inbreeding of $1/(4N)$ is the lowest possible for a population of N breeding individuals, but can be achieved only with $M = F$. With more females than males, *i.e.*, $F = Md$ and $d > 1$, only M male offspring are required but there are F females that can contribute a male offspring. Hence, M females will contribute a male and receive a higher contribution than the $F - M$ females that do not contribute a male. Consequently, $\sigma_r^2 > 0$ and $\Delta F > 1/(4N)$.

Consider a pedigreed population with discrete generations where breeding success among offspring of individual parents is managed, allowing the categorization of parental success. For example, for M males and $F = Md$ females in the scheme of Gowe *et al.* (1959), denoted hereafter as system "G" (see Figure 1a), there are three categories:

1. M male parents, with 1 male and d female offspring each;
2. M female parents, with 1 male and 1 female offspring each;
3. $F - M$ female parents, with 1 female offspring each.

Note that only the sex of the breeding offspring and not the category to which the selected offspring should belong is prescribed. The allocation of the available categories among females is at random. Each of the males is mated to a randomly chosen female from each category.

The expectation and variance of contributions from individual parents can be considered as conditional on either their category (μ_j, σ_j^2, $j = 1, 2, 3$; see Table 1) or their sex (*e.g.*, μ_F, σ_F^2; see Table 1). Since there are two categories of female parents, then, using standard results on conditional and unconditional means and variances,

$$\mu_F = E[\mu_j | j \text{ female category}],$$

$$\sigma_F^2 = E[\sigma_j^2 | j \text{ female category}] + V[\mu_j | j \text{ female category}].$$

For Gowe *et al.* (1959),

$$\begin{aligned} \mu_M &= \mu_1 = (2M)^{-1}, \quad \sigma_M^2 = \sigma_1^2 \\ \mu_F &= d^{-1}\mu_2 + (1 - d^{-1})\mu_3 = (2F)^{-1}, \\ \sigma_F^2 &= d^{-1}\sigma_2^2 + (1 - d^{-1})\,\sigma_3^2 + V_\mu, \end{aligned} \tag{2}$$

where $V_\mu = d^{-1}\mu_2^2 + (1 - d^{-1})\mu_3^2 - \mu_F^2$ is the variance of the mean contribution of the female categories.

Noting that the contribution of any breeding individual accounts for one-half of the contributions of its offspring, the above expectations and variances can be written as

$$\begin{aligned} \mu_1 &= (2M)^{-1}, & \sigma_1^2 &= \tfrac{1}{4}d\sigma_F^2 + \tfrac{1}{4}\sigma_1^2 \\ \mu_2 &= (4M)^{-1} + (4F)^{-1}, & \sigma_2^2 &= \tfrac{1}{4}\sigma_F^2 + \tfrac{1}{4}\sigma_1^2 \\ \mu_3 &= (4F)^{-1}, & \sigma_3^2 &= \tfrac{1}{4}\sigma_F^2. \end{aligned} \tag{3}$$

Together with the equation for σ_F^2 in (2), there are four equations for four unknowns, *i.e.*, σ_1^2, σ_2^2, σ_3^2, and σ_F^2, and these can be solved as a set of simultaneous equations. Solving first for V_μ (using the known μ_2, μ_3, and μ_F) gives $V_\mu = (1 - d^{-1})/16FM$, and after solving the simultaneous equations for the variances σ_1^2, σ_2^2, σ_3^2, and σ_F^2, we obtain

$$\sigma_F^2 = \frac{3}{32}\frac{(1 - d^{-1})}{FM} \quad \text{and} \quad \sigma_M^2 = \frac{1}{32}\frac{(1 - d^{-1})}{M^2}.$$

Using results of Woolliams and Bijma (2000), ΔF can be derived as either $\frac{1}{4}\Sigma_{\text{category } j} X_j(\mu_j^2 + \sigma_j^2)$ or $\frac{1}{4}[M(\mu_M^2 + \sigma_M^2) + F(\mu_F^2 + \sigma_F^2)]$, to give

$$\Delta F = \phi_G/16M, \quad \text{where } \phi_G = (1\tfrac{1}{2} + \tfrac{1}{2}d^{-1}), \tag{4}$$

which is a well-known result (*e.g.*, Falconer and Mackay 1996). For a fixed number of males (M), ΔF decreases when d increases (*i.e.*, when the number of females increases).

In the scheme of Wang (1997), the female contributing a male offspring does not also contribute a female offspring, but instead that female offspring is allocated to another female contributing two female offspring. The result of Wang (1997) with random mating can be derived from an analogous analysis, after noting that there are four categories. This scheme is denoted hereafter as system "W" (see Figure 1b):

1. M male parents, with 1 male and d female offspring each;
2. M female parents, with 1 male offspring each;
3. $F - 2M$ female parents, with 1 female offspring each;
4. M female parents, with 2 female parents each.

For this scheme:

$$\mu_1 = (2M)^{-1}, \quad \mu_2 = (4M)^{-1}, \quad \mu_3 = (4F)^{-1}, \quad \mu_4 = (2F)^{-1}$$

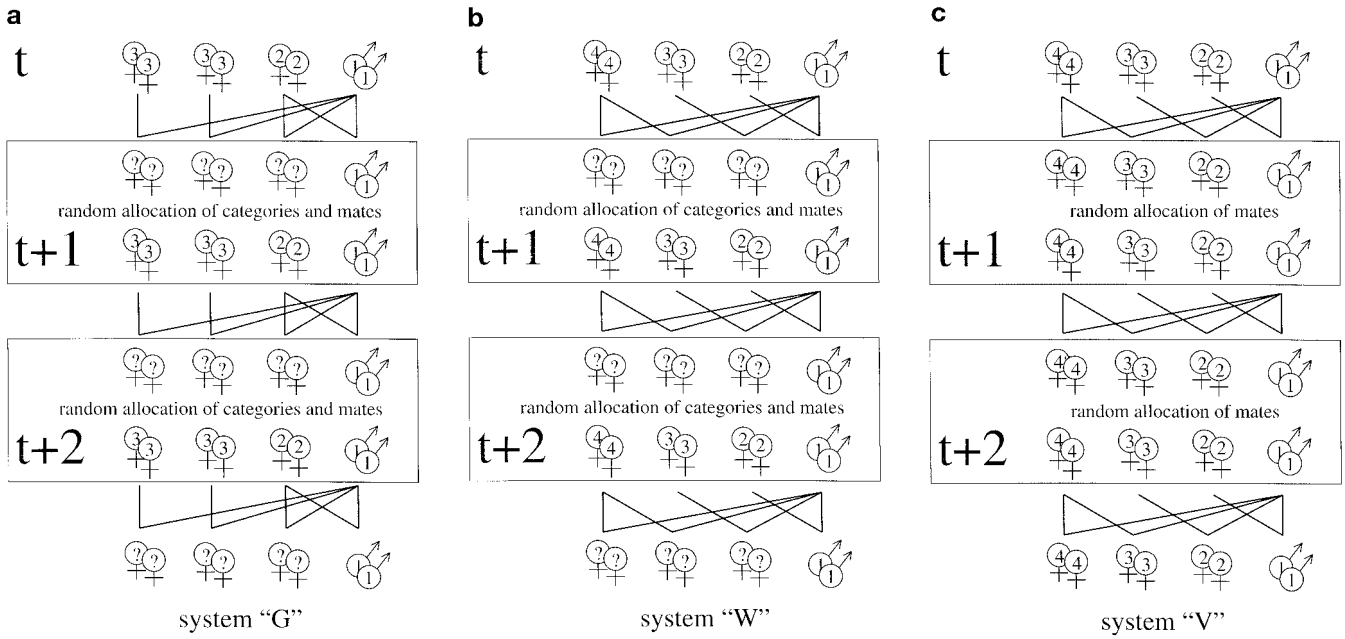

FIGURE 1.—Lineages according to different systems of management: (a) system G of GOWE *et al.* (1959), (b) system W of WANG (1997), and (c) system V in this study, with three generations (t) and two sires and six dams per generation, *i.e.*, with a mating ratio (d) of three dams per sire. Overlapping symbols for male and female shows that females of different categories may mate different males. Boxes enclose the same set of individuals before (top rows with "question-marked" symbols in G and W) and after the breeding categories have been allocated (randomly or directly) to each parent.

$$\sigma_1^2 = \tfrac{1}{4}d\sigma_F^2 + \tfrac{1}{4}\sigma_1^2, \quad \sigma_2^2 = \tfrac{1}{4}\sigma_1^2, \quad \sigma_3^2 = \tfrac{1}{4}\sigma_F^2, \quad \sigma_4^2 = \tfrac{1}{2}\sigma_F^2$$

$$\sigma_F^2 = d^{-1}\sigma_2^2 + (1 - 2d^{-1})\sigma_3^2 + d^{-1}\sigma_4^2 + V_\mu,$$

where $V_\mu = (1 - d^{-1})(d - 2)/16FM$.

Explicit solution of the five equations for the five unknown variances σ_1^2, σ_2^2, σ_3^2, σ_4^2, and σ_F^2 gives

$$\sigma_F^2 = \frac{3}{32}\,\frac{(1 - d^{-1})(1 - 2d^{-1})}{FM},$$

$$\sigma_M^2 = \frac{1}{32}\,\frac{(1 - d^{-1})(1 - 2d^{-1})}{M^2},$$

with

$$\Delta F = \phi_W/16M, \quad \text{where } \phi_W = (1\tfrac{1}{2} - \tfrac{1}{2}d^{-1} + d^{-2}). \qquad (5)$$

Unlike GOWE *et al.* (1959) for a fixed number of males, ΔF decreases up to $d = 4$ and then increases in system W (*i.e.*, adding more females increases ΔF), with the limiting forms for $d = 1$ and $d \to \infty$ being identical to GOWE *et al.* (1959).

In systems G and W, minimizing ΔF is based upon minimizing the variance of the change in frequency of a neutral allele in the population over a single generation ($\sigma^2_{\Delta q}$), using the relationship that $\Delta F = \sigma^2_{\Delta q}/[2q(1 - q)]$ (FALCONER and MACKAY 1996). Although this is the prevailing approach in quantitative genetics, it is valid only when the choice of parents in any generation is independent of all other generations. With this approach, reducing ΔF depends on reducing the variance of the weighted contributions of breeding individuals to the next generation (HILL 1979), *i.e.*, on the variance of weighted family size, $c_i = \frac{1}{2}(M^{-1}m_i + F^{-1}f_i)$, where m_i and f_i are the number of male and female offspring of breeding individual i. W yields lower ΔF than G, because it creates a negative covariance between the number of male and female offspring of a breeding individual, which reduces the variance of c_i. However, there is no proof that W achieves the lowest possible ΔF.

One component of ΔF in G and W is V_μ (in fact, $\Delta F = \frac{1}{4}\Sigma X_j\mu_j^2 + \frac{1}{4}FV_\mu$, result not shown), the variance of the long-term contributions of parents, which arises from the uncertainty over the future contributions of offspring. For example, in W, a category 4 female (with two breeding female offspring) may be the grandparent of two males or both the grandparent of a male and the great-grandparent of a male (see Figure 2). This creates a serious problem for $d > 2$ in which case the contribution of a female is very largely determined by if, and when, a sire occurs among her descendants [*i.e.*, the expected contribution provided by the sire alone is $(\frac{1}{2})^{s+1}M^{-1}$, where s is the number of generations of descendants before the male is born].

The ultimate solution to minimize ΔF comes from considering multiple generations and long-term contributions, using Equation 1. Unlike c_i above, the long-term contribution measures the ultimate contribution of a breeding individual to the gene pool (WOOLLIAMS *et al.* 1999), extending beyond the next generation. Management of contributions over multiple generations avoids the uncertainty shown for G and W over future contributions of offspring and allows us to derive the minimum possible ΔF. In the APPENDIX, we show that the lowest possible ΔF for any population with different numbers of breeding males and females is $\Delta F = \phi/16M$, where $\phi = \frac{4}{3}[1 + 2(\frac{1}{4})^d]$. We present a breeding system (denoted V) that achieves this minimum.

System V (see Figure 1c) has $d + 1$ categories of breeding individuals, one male category and d female categories. Those categories are as follows:

1. M male parents, with 1 male and d female offspring each;
2. M female parents, with a male offspring each;

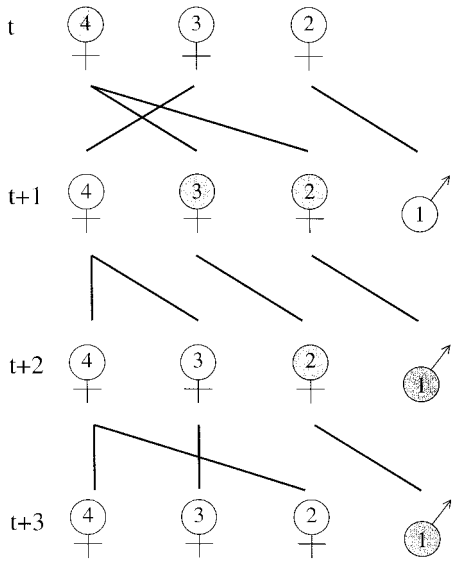

FIGURE 2.—Example of female lineages following system W of WANG (1997), where the mating sires were omitted for simplicity. The lineage with solid symbols represents a category 4 female at generation t that is both the grandparent of a first male and the great-grandparent of a second male. The same category 4 female might have mothered two category 2 females, being in that case the grandparent of two males (example not shown).

3. M female parents, with 1 category 2 female offspring each;
. . .
d. M female parents, with 1 category $d-1$ female offspring each;
$d+1$. M female parents, with 1 category d female and 1 category $d+1$ female offspring each.

In V, each male is mated to a single female from each category. Note that with $d = 2$, V gives identical ΔF to WANG (1997). Unlike previous schemes G and W, with scheme V both the sex and the category of each breeding offspring are prescribed automatically *ad infinitum* along the lineages. An analogous analysis to previous schemes shows for V that

$$\mu_1 = (2M)^{-1}, \quad \mu_2 = (4M)^{-1} \ldots \mu_d = (2^d M)^{-1}, \quad \mu_{d+1} = (2^d M)^{-1}$$

$$\sigma_1^2 = \frac{1}{4}\sum_{j=1}^{d+1}\sigma_j^2$$

$$\sigma_2^2 = \tfrac{1}{4}\sigma_1^2, \quad \sigma_3^2 = \tfrac{1}{4}\sigma_2^2, \quad \sigma_d^2 = \tfrac{1}{4}\sigma_{d-1}^2$$

$$\sigma_{d+1}^2 = \tfrac{1}{4}\sigma_d^2 + \tfrac{1}{4}\sigma_{d+1}^2. \qquad (6)$$

The $d+1$ equations in $d+1$ unknowns (*i.e.*, σ_j^2, $j = 1, \ldots, d+1$) have a unique solution with $\sigma_j^2 = 0$; *i.e.*, there is not variance of contributions within categories. Thus by following this scheme the only variance attached to genetic contributions is the variance among category means. Finally

$$\Delta F = \frac{1}{4M}\left[\sum_{j=1}^{d} 1/2^{2j} + 1/2^{2d}\right]$$
$$= \phi_V/16M \quad \text{where } \phi_V = \tfrac{1}{3}[1 + 2(\tfrac{1}{4})^d].$$

The rationale behind V is as follows. For any population with $F = Md$ females, it takes at least d generations before each female has a male descendant. V has d female categories, and within d generations each female category produces male descendants. Hence, V distributes male descendants as equally as possible among females. With V, ΔF decreases monotonically in d, approaching $1/(12M)$ for large d. V avoids the disturbing property of W that ΔF increases as females are added to the population.

Corrections to predictions: WOOLLIAMS and BIJMA (2000) showed that predictions based on long-term contributions are expected to underestimate ΔF by a proportion of $-2\Delta F$. Therefore all predictions of ΔF presented are scaled from those above by $(1 + 2\Delta F)$; *i.e.*, $\Delta F'$ is presented where $\Delta F' = (1 + 2\Delta F)\Delta F$, and ΔF is as given above. It is important to note, however, that the adjustment from ΔF to $\Delta F'$ is of second order, and unadjusted predictions made via contributions are identical to those provided by, for example, HILL (1979) and WANG (1997).

Monte Carlo simulations: To check the accuracy of the predicted rate of inbreeding, each of the systems of management described above was simulated stochastically. Each simulated population was composed of 40 discrete, nonoverlapping generations, with $M = 4$ males and $F = Md$ females per generation ($d = 1, 2, \ldots, 20$ dams per sire). The number of male and female offspring per dam was determined according to each dam's category, following one of the above systems of management. Each breeding male was mated to d randomly selected females. Nonrandom mating was addressed also by simulation for a limited number of cases of system V. Further details concerning nonrandom mating are given below in the DISCUSSION. The inbreeding coefficient was calculated from the pedigree relationships, and the asymptotic rate of inbreeding was obtained as the average over the last 20 generations of each simulated pedigree. Each simulation was composed of 500 replicates.

RESULTS

Rates of inbreeding obtained from the above equations for G, W, and V are presented in Figure 3 as a function of d, together with rates of inbreeding obtained from simulated pedigrees. Results from simulations agreed very closely with predicted values from the three systems. Although predicted ΔF made via contributions depends on M and d according to Equations 4–6, the differences in ΔF between any two systems for a given d do not depend on M. Therefore, current comparisons with $M = 4$ are fully applicable to any other M. Considering first system G *vs.* V in terms of difference in ΔF $[100 \times (\Delta F_G - \Delta F_V)/\Delta F_V]$, the maximum is attained with $d = 3$ (21.2%) and then decreases rapidly in d approaching asymptotically a value of 12.5% ($d \to \infty$). Considering now system W *vs.* V in equivalent terms $[100 \times (\Delta F_W - \Delta F_V)/\Delta F_V]$, there is no difference with $d \leq 2$, but it rises rapidly in d (5.1% when $d = 3$, 7% when $d = 4$) with a limiting form identical to G *vs.* V (12.5%, $d \to \infty$).

An illustrative example of the impact the absence of the variance attached to female genetic contributions might have on ΔF is also given in Figure 3 by $1/(16M)(1 + d^{-1})$. This hypothetical minimum ΔF results from the unrealistic assumption that when $F > M$ there is no difference in contribution among female categories, and ΔF would be 33.3% lower than that of system V

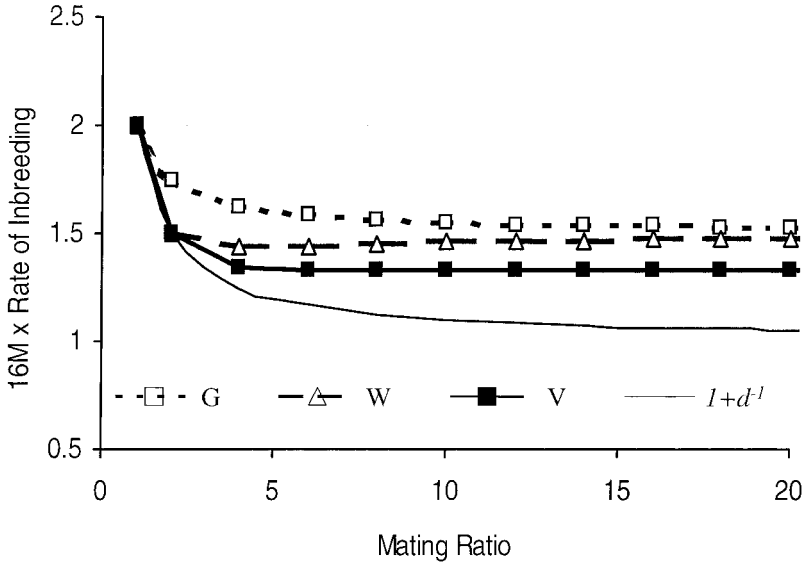

FIGURE 3.—The asymptotic rate of inbreeding by utilizing different systems of management plotted against the mating ratio (d dams per sire), according to predictions made via contributions (lines) or simulations (symbols). The thin solid line is the hypothetical minimum with equally contributing females ($1 + d^{-1}$). The rate of inbreeding is the plotted value divided by $16M$, where M is the number of breeding males.

when $d \rightarrow \infty$. Another example (not shown) comes from unmanaged populations of identical size to those described above, but with Poisson distribution of successful offspring among parents, random mating, and no selection (WRIGHT 1931). In these circumstances, the resulting ΔF would be 100% higher than that of system V when $d = 2$, and it would still show ΔF 50% higher than that of system V when $d \rightarrow \infty$.

DISCUSSION

This article has shown that by managing genetic contributions over generations via the pedigree, using simple methods, schemes can be designed and implemented to achieve $\Delta F = \phi/(12M)$, where $\phi = [1 + 2(\frac{1}{4})^d]$, the lowest possible ΔF with random mating. For simplicity, this assumes (as does the following discussion) that $F \geq M$. The strategy used in V can be viewed as a multigeneration generalization of WANG (1997), where lineages of dams and their genetic contributions are prescribed *ad infinitum* across generations to avoid any uncertainty over offspring contributions. The method gives identical predictions to that of Wang for $d = 2$. However, for $d > 2$ with random mating, the method improves over previous methods and avoids an unsatisfactory characteristic of Wang's strategy, namely that when M is fixed and d increases, *i.e.*, more females are added to the scheme, ΔF increases.

The sum of squared contributions for the V system is $\phi/(3M)$, where $\phi = [1 + 2(\frac{1}{4})^d]$, and the APPENDIX shows that $\phi/(3M)$ must also be the lower bound for the sum of squared contributions in the population; *i.e.*, we have established an achievable lower bound for Σr_i^2. In general, $\Delta F = \frac{1}{4}(1 - \alpha)\Sigma r_i^2$ (WOOLLIAMS and BIJMA 2000), where α is the deviation from Hardy-Weinberg equilibrium (CABALLERO and HILL 1992), which measures the departure from the random union of gametes in the gene pool. Deviations from Hardy-Weinberg equilibrium indicate preference for ($\alpha > 0$) or avoidance of ($\alpha < 0$) matings between relatives. Because V achieves the lower bound of Σr_i^2, it yields the minimum possible ΔF for any α. This can be seen by noting that the result of WOOLLIAMS and BIJMA (2000) is a complete description of ΔF that accounts for any specific mating strategy for parents. As a special case, we have shown that when $\alpha = 0$, the minimal $\Delta F \approx 1/(12M)$ for large d is less than the value $3/(32M)$ obtained from considering G or W with large d and $>1/(16M)(1 + d^{-1})$ (Figure 3) that might be assumed to be minimal, on the basis of the erroneous argument that female genetic contributions would all be of order $1/F$.

The inference that follows is that further reductions in ΔF below those presented for random mating in RESULTS can be made only by having ($\alpha > 0$), with mating schemes in system V that preferentially mate relatives. Strictly, the α in the results obtained by simulation was very slightly negative due to the division of the gene pool into two sexes. This inference for preferential mating of relatives may seem counterintuitive because many studies of populations, whether directionally selected or managed for conservation, suggest that implementing preferential mating of relatives ($\alpha > 0$) increases ΔF (CABALLERO and HILL 1992; CABALLERO *et al.* 1996; WANG 1997). However, the condition for preferential mating of relatives to reduce ΔF is that it should not increase Σr_i^2 by a factor greater than the factor it reduces the term $(1 - \alpha)$. The observation that preferential mating of relatives can reduce ΔF has been described before (CABALLERO 1994), but only for the special case of $d = 1$ ($M = F$) and where $m_i = f_i = 1$ causes Σr_i^2 to be fixed. Note that this corresponds to the rule of son replacing his sire and daughter replacing her dam that

leads to absence of variance attached to genetic contributions among parents. The resolution of this issue comes from observing that G and W still have substantial variance of long-term contributions among breeding males and among breeding females, since they attempt to manage contributions only to the descendant generation, *i.e.*, c_i. In W, for example, the coefficient of variation of the sire contribution varies from 0.17 to 0.35 as d moves from 3 to ∞ (see MATERIALS AND METHODS). The imposition of $\alpha < 0$ in G and W by avoiding matings between relatives (i) reduces the potential ΔF by removing unnecessary variation within breeding categories, *i.e.*, by promoting the mixing of lineages, which reduces genetic drift and therefore also Σr_i^2, and (ii) increases the potential ΔF by encouraging heterozygosity (CABALLERO 1994), since $(1 - \alpha) > 1$. WANG (1997) demonstrates that the impact of the first effect more than offsets that of the second. According to the same reasoning, the imposition of $\alpha > 0$ in G and W would have adverse consequences on ΔF.

The system V, however, has no variance for long-term contributions, other than those defined by the category, so that $\alpha < 0$ can have no benefit. Given the category of an individual, random drift in V originates solely from Mendelian sampling of alleles. The amount of drift due to Mendelian sampling decreases with increasing α, because an increase in α reduces the proportion of heterozygote individuals in the population. Our results are consistent with those presented by WANG (1997). For example, for $M = 4$, $d = 3$, V with only random mating has $N_e = 23.3$, compared to 21.4 for W with herd-based half-sibs avoidance (termed NM by Wang) or minimum coancestry mating. Analysis of Equation 9 of WANG (1997) shows that ΔF for W with NM approaches $1/(12M)$ for large d, which is the same as V (with $\alpha = 0$, a suboptimal α for V) but at a slower rate.

Additionally, by writing $\Delta F = \frac{1}{4}\Sigma r_i^2(1 - \alpha_i)$ we can predict which mating has the biggest impact on ΔF in the scheme V. We have verified by simulation that mating category 2 females to their male half-sibs is the most powerful single-nominated mating to reduce ΔF, reducing it by 5%. The mating of the same sire to the category 3 half-sib female would be the next additional step.

Partial-sib mating has been suggested as a way of purging genetic load (TEMPLETON and READ 1984; CABALLERO and SANTIAGO 1995). However, the utility of purging deleterious and detrimental alleles by preferential mating of relatives ($\alpha > 0$) is a contentious issue in conservation genetics (HEDRICK 1994; FRANKHAM 1995; LACY and BALLOU 1998; VISSCHER *et al.* 2001; FRANKHAM *et al.* 2002). Previous solutions to minimize ΔF in populations with different numbers of males and females are in conflict with the requirement for purging, because it increases long-term ΔF. With V, however, purging ($\alpha > 0$) reduces ΔF, thereby removing the trade-off between purging and long-term genetic diversity. However, purging should be considered carefully, since it may reduce fitness due to short-term inbreeding depression.

Scheme V has important implications for the conservation of wild captive species and rare domestic breeds of livestock. Populations with 5–20 males or 100–1000 females, for example, are classified as endangered by FAO (2000). When applying V, populations of at least 9 breeding males have the potential to be genetically viable according to FAO criteria (FAO 1998; *i.e.*, $\Delta F < 1\%$). For any desired ΔF, the classical solution (WRIGHT 1938) requires 50% more breeding males than V requires when there is no stringent restriction on the number of breeding females.

All the results derived in this study apply to chromosomal DNA only, not to mtDNA. The study has not considered (i) overlapping generations, but with no selection the V schemes should generalize in a straightforward manner, and (ii) the addition of molecular tools, which may enhance the sampling of individuals within families (WANG 2001). Additionally the study has not considered the application of selection tools in conservation of genetic resources (GRUNDY *et al.* 1998b; SONESSON and MEUWISSEN 2001), although GRUNDY *et al.* (1998b) showed that these tools are also essentially minimizing the sum of squared contributions among the candidates. CABALLERO *et al.* (1996) suggest that algorithms such as minimum coancestry selection and mating achieve the best possible means for reducing ΔF, but this work clearly shows this is *not* the case. Practical implementation of system V in conservation would demand that rules for nonavailability of offspring or offspring of the right sex may be required, and such a development has not been considered in this article. Consideration of the argument in the APPENDIX may lead to rules that are simply applied, and other approaches may prove to be more robust, yet the simplicity of the argument in the APPENDIX is highly valuable for general understanding. This study has established minimum lower bounds for inbreeding rates that are achievable through pedigree recording alone. The major step in accomplishing this task was the management of long-term contributions over multiple generations.

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APPENDIX: A LOWER BOUND FOR THE RATE OF INBREEDING

In general (Woolliams and Bijma 2000), $\Delta F = \frac{1}{4}(1 - \alpha)\Sigma r_i^2$. For any α, therefore, ΔF is minimized by minimizing Σr_i^2. First consider the contribution for males alone. The Σr_i^2 is minimized when each of the M males contributes equally, so that each $r_i = 1/(2M)$, because males contribute only half the gene pool. Next, consider the contributions of the F females, traced through maternal lineages until they have male descendants. Any population with $F = Md$ females must have (i) M dams of sires, each contributing $1/(4M)$ via their son, and (ii) M dams of dams-of-sires, each contributing $1/(8M)$ via their maternal grandson, etc.

In general, $a^2 + b^2 < (a + b)^2$ for any $a, b > 0$. The Σr_i^2 is minimized therefore when (i) the M dams of sires are distinct individuals, (ii) these M dams are distinct from the M dams of dams-of-sires, and (iii) the M dams of dams of-sires are distinct individuals also. This distinction of roles among the Md female parents can continue for d generations, *i.e.*, until each female produces a male within d generations. This allocation process accounts for a total Σr_i^2 of $M[1/(4M) + 1/(8M) + 1/(16M) \ldots] = \frac{1}{2} - 1/(2^{d+1})$.

The total contribution of the F female parents is $\frac{1}{2}$. Thus $1/(2^{d+1})$ is unaccounted for by the allocation process described above and must be allocated among the F femaleparents so that Σr_i^2 is minimized. Given the inevitable unequal contributions due to the allocation process, Σr_i^2 is minimized when the remaining contribution is allocated to the females with the lowest contribution, under the condition that their final individual contribution does not exceed that of any other female. Thus, allocating the remaining $1/(2^{d+1})$ equally among those females that produce males after d generations minimizes Σr_i^2. It increases the contribution of these females to a value of $1/(2^d M)$. Note that system V reproduces this allocation process.

As a minimum, therefore, we have M males, each contributing $1/(2M)$; M females, each contributing $1/(4M)$; M females, each contributing $1/(8M)$, etc.; but $2M$ females, each contributing $1/(2^d M)$. This yields a minimum sum of squared contributions of $[M/(2M)^2] + [M/(4M)^2 + M/(8M)^2 + \ldots + 2M/(2^d M)^2]$, to give a lower bound of $\Sigma r_i^2 = \phi_V/(4M)$, where $\phi_V = \frac{4}{3}[1 + 2(\frac{1}{4})^d]$. In general, $\Delta F = \frac{1}{4}(1 - \alpha)\Sigma r_i^2$, so that for any α, $\Delta F \geq (1 - \alpha)\phi_V/(16M)$. For large d and random mating, the lower bound for ΔF approaches $1/(12M)$. This article shows that system V achieves this lower bound for all d.